III. *Remarks on the Nature of the outer fleshy covering of the Seed in the* Clusiaceæ, Magnoliaceæ, *&c., and on the Development of the Raphe in general, under its various circumstances. By* John Miers, *Esq., F.R.S., F.L.S., &c.*

Read March 18th, 1856.

In a notice read before the Linnean Society on the structure of the seed of the *Clusiaceæ*, I described the external fleshy envelope of the seed of the *Clusieæ*, and offered evidence to prove that this coating is a product of extraneous placentary growth, subsequent to the development of the primine, and therefore a kind of arillus. It was of some importance to ascertain this point, as in the tribe *Tovomiteæ* of the same family, the outer coating, similar in substance and colour, is unquestionably an aril: this is manifest from its peculiar form; it is free from the testa, but may be opened out like a flat plate; it is folded round the seed which it envelopes and conceals, its margins being free and overlapping one another: in the other tribe of the *Garcinieæ*, this covering is also entire, is soft, and assumes the character of an enveloping pulp. If, therefore, in the two latter tribes, the outer coating be unquestionably an aril, it was fair to conclude that the analogous envelope in the *Clusiaceæ* is of a similar nature. This inference was still farther confirmed by the presence of a distinct simple raphe, which extends from the base to the apex of the seed beneath the inner pellicle of the aril; it lies within a groove of the testa from which it is wholly free, the apex of which it perforates, and becomes lost in the chalaza of the inner integument. Under the evidence of such demonstrative proof, as far as regards the *Clusieæ*, I was led to institute a comparison of similar facts observable in the *Magnoliaceæ*, because, if that coating be considered an aril in the one family, it must be of the same nature in the other. I then referred to the admirable work of Dr. Asa Gray ('The Genera of the Plants of the United States'), where a different view is entertained: here the external fleshy coat of the seeds of *Magnolia* is described as the testa, and its thick bony shell as the tegmen, or inner integument, the true tegmen having escaped the notice of that excellent botanist. In opposition to this view, I referred to the analysis I had made many years before, of the seed of *Talauma*, a genus intimately allied to *Magnolia*: the evidence then collected, convinced me that the 'testa' described by Dr. Gray is arilliform, and that his 'tegmen' is the true testa. If we examine this outer coating in *Talauma*, where it is entire, we find it easily detached from the testa or osseous shell; and if we begin to pull it away from the summit, the raphe, as a distinct cord, will be seen quite free from it, as in the *Clusieæ*, and to lie in a corresponding groove which extends from the base to the apex: the upper end of this raphe is seen to penetrate an aperture near the summit of this osseous shell, and to become lost in the dark-coloured chalaza of a membranaceous inner integument. To all appearance, the raphe thus seems quite free; but if we examine it more attentively, a corresponding portion of the extremely

delicate inner pellicle of the aril will be found attached to it, which has been torn away by the raphe. After detailing these facts, I proceeded to show that the nature of the different coats of the seed may be always determined, with certainty, by the relation of one with the other, and from the position they bear in regard to the raphe and the chalaza of the inner integument, and that wherever the raphe is found outside the testa, any tunic exterior to the latter must be of a growth posterior to the development of the original coats of the ovule. From the position of the raphe in the seeds of *Magnolia* and *Talauma*, I consequently drew the infallible deduction, as it appears to me, that the more external fleshy envelope must be arilliform, the thick osseous nut must be the testa, and the inner integument with its thickened chalaza must be the true tegmen.

Since the reading of the above memoir, the first volume of that truly excellent work, the 'Flora Indica' of Dr. Hooker and Dr. Thomson has appeared, in which they detail the nature of the outer tunics of the seed of *Magnolia* (in p. 73), entirely in accordance with the conclusion of Dr. Asa Gray, but the reasons on which they have adopted this conclusion appear to me to involve some points which materially affect the legitimacy of the inferences there deduced. I cannot agree in their opinion of the perfect accuracy of the account of the structure of the seed of *Magnolia*, as given by Gærtner, for though nothing contrary to truth is there stated, yet the most important point which bears on the present discussion, the existence of a raphe, is altogether omitted; and I feel convinced, that if that eminent carpologist had been aware of its existence, he would not have concluded that the outermost coating forms one of the true integuments of the seed, meaning by this term, those which are developments of the primine, secundine, &c. The authors of the 'Flora Indica' and the distinguished American professor do not notice the peculiar perforation in the summit of the crustaceous envelope through which the raphe passes, and they call this extremity the chalaza, a term which, in accordance with Gærtner, I think ought always to be restricted to that peculiar thickening of the inner integument around the point where the raphe becomes lost in its substance*. I have minutely described this process of the testa in the seed of *Talauma* as a distinct perforation which I have called the diapyle; it is of frequent occurrence in the extremity of the testa of the seeds of different plants, and is destined solely to the purpose just mentioned; in fact it is the corresponding point in the original base of the primine through which the spiral vessels, represented in the figure of Dr. A. Gray, pass to communicate their nourishing influence to the secundine, and to the body of the ovule, prior to the commencement of its inversion, and is the only point in the primine in which there exists any passage for these vessels, either before or after the anatropal action, and therefore the only point in the testa (or tunic, resulting purely from the growth of the primine), that could be traversed by the raphe. The presence of a diapyle in one of the tunics of a seed, is as certain an indication that this is the real testa, as the existence of a chalaza affords the surest proof of the nature of the inner integument. The actuality of the true chalaza,

* "Chalaza nempe nobis dicitur parva areola saturatè colorata, aut tuberculum parvum spongiosum, aut callosum, quod ex ultimis vasorum umbilicalium internorum finibus, vel et ex chorii exsuccis reliquiis originem suam trahit, et in superficie exteriore membranæ seminis internæ conspicitur."—*Gærtn. de Fruct., Introd.* p. 135.

and its connexion with the raphe, in the relative position in which the latter is found, have evidently escaped the observation of these eminent botanists, as they had previously done that of Gærtner; it is, however, important to attend to these distinctions, as they form essential and convincing elements in this inquiry.

Still more recently a paper from Dr. Asa Gray has appeared in 'Hooker's Kew Journal of Botany' (vol. vii. p. 243), "On the Development and Structure of the Integument of of the Seed of *Magnolia*." This was written in reply to my observations on the arilliform nature of the outer tunic, to which I have above referred. In that note, this accomplished botanist warmly defends his former opinion, which he maintains with great ingenuity and candour, but I find nothing there stated that disproves the conclusion of most botanists, regarding the nature of the several seminal tunics in question, which I have here endeavoured to confirm. If I had not been convinced that the issue admits of the most simple and demonstrative proof, I should not have presumed to contest the united authority of the distinguished American professor, and of the highly talented authors of the 'Flora Indica,' whose opinions are entitled to especial consideration.

The argument that the scarlet external envelope cannot be an aril, because the latter "must needs have an opening at the top," stands upon very feeble ground. This was the definition of St. Hilaire, who classed the different forms of arilliform coatings under two denominations: 1. the true aril where the envelope has an opening in the top; 2. the false aril, where the coating that surrounds the testa is entire. Dr. Planchon, however, who ably defended and extended the views of his friend, in regard to the nature and origin of the aril, has shown that this definition does not hold good, and among other cases, he cites a species of *Tetracera* from Java, where the perfectly true aril forms an entire tunic. I need hardly refer to Gærtner, who also divides the aril into two kinds, the complete and the incomplete; notwithstanding that in some of the instances of the first kind, he has mistaken the endocarp for an aril; others, which he enumerates, possess a complete arilliform covering, among them *Nephelium*, which in this respect offers a good analogy with *Magnolia*. Another instance is still more remarkable, because it is recorded by Dr. A. Gray himself, in the same admirable work, and within a few pages of his description of *Magnolia*: it occurs among the *Anonaceæ*, figured in the genus *Asimina*, (plate 27) and described (p. 57) as entirely covering the testa, without the mention of any aperture in the apex. There is indeed no reason why an aril, which is a development from the placenta, may not form an entire coating, as well as the true integuments of the seed, originally cup-shaped processes. The argument of the inadmissibility of an aril, because it is not open at the top, therefore completely fails.

In regard to the remaining arguments of Dr. A. Gray, I can only repeat what has just been demonstrated, that the nourishing vessels from the placenta, as he has figured them, only penetrate the primine of the ovule of *Magnolia* at the gangylode*; they cannot and do not enter at the opposite extremity; but if we examine the ripe seed, we find the

* For the sake of demonstration I have here given the name of gangylode to that common point of union of the primine, secundine and tercine in the original base, now the summit of the inverted ovule, which afterwards form the diapyle of the testa, and the chalaza of the inner integument of the seed.

vessels of the raphe penetrating the outer coating at the hilum, that is to say, at the extremity diametrically opposite to that of the original gangylode, and after running along its inner surface, they find their way straight to the diapyle of the enclosed nut, through which they pass to lose themselves in the chalaza of the inner integument, both which points in the ripe seed (the diapyle and chalaza) correspond with the gangylode of the ovule.

I have endeavoured, by the accompanying figures, to render this question manifest. Plate XIX. figs. 56 & 57 represent an ovule of *Magnolia* after Dr. A. Gray, showing the broad placentary sheath which encloses the spiral vessels of the raphe. Fig. 58 is a longitudinal section of the same, showing that the spiral vessels originate at the placenta and hilum, and that they terminate at the opposite extremity, at the point of the gangylode, which is the only point of the primine where these vessels traverse, in order to convey nutrition to the secundine and nucleus: it is here evident that the sheath or extension of the placenta containing these spiral vessels, must always remain exterior to the primine, as well as to the tunic resulting from its subsequent growth. Fig. 59 shows a section of the ripe seed of *Magnolia*, where the placentary sheath (seen in fig. 58) during the increment of the ovule, has in the progress of its own growth, extended itself all over the primine, and has become enlarged into an arilliform scarlet coating, and we have proof that this coating is the result of such growth, by the fact that the raphe, retaining the same position and direction, still remains enclosed in its substance. The primine, during its increment, by the deposition of osseous cells within it, in the manner recorded by Dr. Gray, becomes converted into the bony testa, shown in figs. 60 & 61, where the diapyle or aperture is seen in its apex for the passage of the raphe, corresponding with the same point of the gangylode in the ovule, through which these same vessels there penetrated: we have evidence that this testa is the product of the primine, not only from this circumstance, but because it is exterior to another integument, the tegmen, which covers the albumen, and which exhibits a chalaza in its apex, as seen in fig. 62. The above gives us an example of the development of the simple raphe.

As an instance of a branching raphe, I will select the seed of *Licania*, shown in fig. 63; this has a basal hilum, and is the growth of an anatropal ovule. Referring to figs. 56 & 58, it is evident that the only point where the spiral vessels can enter the primine, is at the gangylode, the point which they passed through prior to the inversion of the ovule. If, therefore, under the hypothesis of Dr. Gray, the raphe insinuated itself into the substance of the primine, it must, in the case of *Licania*, begin to send out its ramifications from the point at which it entered, that is to say, from the gangylode; but on the contrary, we find that all the vessels start from the opposite point of the hilum: the main bundle directs a straight course (as in the case of the simple raphe) to the gangylode or chalazal point, throwing out its redundant vessels in many lateral branches, while other principal bundles start also from the hilar point, and spread themselves by continual subdivision all over the surface of the seed. Now it is clear, if these vessels were imbedded simply within the primine, or in the tunic resulting from its growth, that they must have escaped from the placentary sheath and have pierced their way through the outer pellicle of the primine, and insinuated themselves into its substance at a point near the micropyle,

a supposition that cannot be entertained for a moment. As therefore the spiral vessels, at the period of the inversion of the ovule, starting from the hilar point, must have been contained within a simple sheath, an extension of the placenta, and as these vessels during the subsequent growth of the ovule, are found to ramify from this point over its whole surface, it is clear that the sheath which contains them must have become here extended with them, in the same manner, as has been ascertained by actual observation, that it really does grow over the primine in other cases.

This may be rendered still more palpable by reference to a simple model. This mode of demonstration was first ingeniously suggested by St. Hilaire in his 'Leçons de Botanique' (p. 541), and I will here repeat it with some modifications. Let us suppose a simple flower with a tubular calyx, closed before æstivation, enclosing a tubular corolla, which again invests a superior ovary: we have here a good illustration of an erect ovule, the calyx representing the primine, the corolla the secundine, and the pistil the main body of the ovule or nucleus. Let us farther conceive the same floral model supported on a pedicel of equal length, and that the flower be suddenly bent down upon its pedicel, becoming glued to the calyx: we have thus an excellent representation of an anatropal ovule, where the former base of the flower is now become its summit, and *vice versâ*; the calyx, corolla, and pistil still remain the analogues of the primine, secundine, and body of the ovule: the foot of the calyx or torus, through which the nourishing vessels pass to promote the growth of the several parts, corresponds to the spot I have called the gangylode, and the adherent pedicel will represent the nourishing vessels enclosed in form of a sheath, or extension of the placenta, and the origin of the future raphe. It is evident, that during the subsequent growth of these tunics, this raphe must always remain exterior to the primine, as we see it in this model. Now if, as it has been contended by Dr. A. Gray, the arilliform coat of the seed of *Magnolia* be only the primine of the ovule enlarged in growth, and if, as he admits, the raphe be found within this coating, it is evident, referring to our model, that the pedicel must have become detached from the calyx, and made to penetrate not through the original point of its attachment to the torus (corresponding with the gangylode), but in some unaccountable manner, and for no purpose, must have pierced its way through the calyx near its summit (at a spot corresponding to the hilum in the ovule), and thus have insinuated itself inside the calyx, traversing its whole length in order to form a new line of communication of the vessels proceeding from the base of the pedicel to the torus, within, instead of without, the calyx: this is so manifest an improbability, as to carry conviction in the simple statement of the fact.

Doctor Asa Gray now candidly confesses that he had overlooked the existence of the inner integument, and therefore the true chalaza, and to avoid the intricacies into which this admission would naturally lead him, he has, in great measure, renounced his former argument of considering the fleshy covering and the crustaceous nut, the one as a product of the primine, the other of the secundine, and has now most ingeniously substituted an entirely new view of the subject, suggesting that these two seminal envelopes constitute in fact one coating, both proceeding from the simple increment of the primine, forming a drupaceous testa; his words are, "the external coat of the ovule becomes drupaceous in

the seed, its outer portion forming the pulpy, the inner the crustaceous seed-coat." This ingenious reasoning cannot however be maintained in view of the real circumstances of the case, for it does not in any degree remove the insuperable obstacle which I have urged against his doctrine, in the position of the raphe with regard to the several coatings of the seed and to the true chalaza. But supposing, for argument's sake, we waive that objection, the reasoning is not tenable upon other grounds, because if such were the origin of these two envelopes, there ought to exist an intimate union of the fleshy exterior with the bony nut, having its several osseous and fleshy deposits enclosed within the two original epidermal pellicles of the primine. We find, on the contrary, that the osseous substance of the nut is furnished internally with a smooth skin, and externally with a distinct hardened epidermis, which in *Talauma* I found to be black and polished in the living state; the fleshy coating is also furnished on both surfaces with a distinct reticulated membrane, the inner pellicle being clearly seen with a lens. The arilliform coating, in every case examined, I have found provided with a double (that is an endodermal as well as an epidermal) membrane, showing it to be a distinct formation from the testa. Although perfectly free from the latter in *Passiflora*, &c., it is generally more or less adherent to it, especially in those cases where the raphe is spread over its whole area in branching ramifications: by its close adhesion to the testa, it then forms a compound tunic, and when the external coating is fleshy and the raphe is simple, as in *Magnolia*, &c., it can often be easily separated from it in an entire state: this is what Gærtner calls, a baccate or fleshy testa*.

My view of the nature of this development is simply the following: that in the act of inversion of the ovule, the spiral vessels destined for its nourishment and always retaining their original attachment to it at the gangylode, are drawn out, together with an enveloping portion of the placenta, so that by means of these spiral vessels and this placentary sheath, the same communication between the placenta and the gangylode of the ovule is maintained that had existed prior to the act of its inversion. This placentary sheath with its enclosed spiral vessels, appears like a prominent broad external band, as shown and figured by Dr. Asa Gray, both in relief and in section, in his analysis of *Magnolia*, to which I have referred: up to this point we are both in accord. This band afterwards becomes expanded by almost imperceptible degrees over the primine, until it finally envelopes it in the manner I shall presently demonstrate: it then becomes thickened by internal deposits, and assumes the form of a distinct scarlet fleshy covering over the testa, being quite arilliform in its structure and appearance. The testa is a distinct development, formed by the secretion of transverse crystalline cells, closely compacted within the substance of the primine, the deposition of which cells has been noticed and recorded by Dr. Gray†. The only circumstance that bears any weight in the opposite

* "Testa carnosa solis competit seminibus baccatis, et respectu situs sui nonnunquam exceptionem a regulâ facit, cum sæpè tertium a nucleo inter integumenta teneat locum; ut in *Bixâ* atque *Magnoliâ*. Hinc proximam cum arillo habet affinitatem, atque hac solâ notâ ab eo discernitur, quod carnosa testa semper arctissimo nexu cum totâ seminis sui superficie cohæreat: ut in modò dictis, nec non in *Gloriosâ*, &c., in quibus nullum inter carnem atque semen ipsum intercedit spatium liberum, sicut in seminibus arillatis *Scytaliæ* (*Nephelii*) et aliarum."—Gærtn. Introd. p. 133.

† Hooker's Kew Journ. Bot. vol. viii. p. 23.

view of the question is one which certainly ought to have its due importance, and is one which I have never doubted in the smallest degree, viz. that Dr. Gray has watched the progress of the growth of the seed from the ovule and could never detect any subsequent or extraneous production over the primine. In the fullest credence of this assertion I still think we have convincing proof that such extraneous growth, though he failed in distinguishing it, must have taken place imperceptibly, in the same way that other observers have witnessed a similar gradual extension over the primine.

The foregoing discussion has induced me to offer a few additional observations on the nature of the raphe. I have been led into this inquiry by the phænomena that present themselves in the *Clusiaceæ*, where I found it difficult to assign a reason, why the raphe should in one case consist of a single cord of vessels, almost in a free state, within the inner pellicle of the external arilliform coating, and wholly free from the testa, as invariably occurs in the *Clusieæ*, while in the *Tovomiteæ*, the raphe has no connexion with the enveloping aril, but appears imbedded in the slender chartaceous testa, not as in the former case like a simple cord, but spread in the form of several branching nervures continually subdividing themselves, and distributed in new ramifications throughout the whole area of the testa. There appears here a difference of structure somewhat inexplicable, but after a little consideration, we may trace to one uniform rule the varying appearances of the raphe under these different forms and position. We owe to the profound investigations of our great countryman Mr. Brown, most of the knowledge we possess regarding the growth and development of the ovule and its original tunics, the changes they undergo during and after the anatropal metamorphosis, the gradual transformation of these tunics into the different coatings of the seed, and the share they afford in the nourishment and development of the growing embryo: but the phænomena attendant on the formation of the raphe, the modifications which these nourishing vessels undergo, and the different modes of their distribution, appear to have excited little notice, for we find few observations on the subject in the works of physiological botanists. On this account I will venture to offer some remarks that have occurred to me in my pending investigation of the *Clusiaceæ*.

Let us now examine some of the circumstances attendant on the inversion of the ovule. Prior to this action, the body of the ovule or nucleus is generally seated within two cups, to which the names of primine and secundine are given: these cups gradually increase in size, and grow into complete tunics which envelope and conceal the nucleus, also called the tercine: during this early stage, the vessels destined to nourish the ovule pass immediately from the placenta into the gangylode or common point which unites the nucleus with the secundine and primine then in contact with the placenta; but during the progress of inversion, the gangylode, as before shown, becomes removed to some distance, and a portion of the placenta is drawn away with it and extended over one side of the primine, at first in the form of an elongated sheath or band, as figured by Dr. A. Gray, carrying with it the spiral vessels proceeding from the placenta and terminating in the now remote gangylode: this placentary extension, whatever form it may assume in its subsequent growth, must always remain outside the primine notwithstanding that it may become agglutinated to it. Now these nourishing vessels may be all compacted in a

single cord, or a portion of them in excess may become branched and extended with the growth of the placentary sheath over the whole surface of the ovule, and thus spread into numerous ramifications; but however they may become thus distributed, they must in all cases remain enclosed within their placentary envelope, and, as above shown, be necessarily exterior to the primine. This placentary sheath, first seen as an adnate longitudinal band, and afterwards extended in the form of a complete investiture over the primine, will be found to assume different phases of development: it may, during this subsequent expansion, be reduced to a degree of attenuation not thicker than a mere skin, and by desiccation of the matters secreted between it and the primine, both may become intimately fastened together, as we know occurs frequently with the primine and secundine, in which case the ramified bundles of vessels would thus become enclosed within this apparently simple, but really compound tunic, presenting a series of anastomosing nervures, such as I have figured in the testa of *Tovomita* and *Commirhea**, and by a careful dissection of this sort of tunic, we find the confirmation of this structure. In other cases, where the nourishing vessels remain compacted in one simple bundle or cord, we may conceive that the placentary sheath, which originally enclosed them, has extended itself over the primine in the manner described, and has become developed in the form of such an arilliform tunic, as we find in the *Clusieæ* and *Magnoliaceæ*, the raphe in such case necessarily remaining quite free from the testa. Inconsistent in result as the two opposite cases just referred to, may at first sight have appeared, it is evident from this explication, that both are in perfect harmony with one simple and uniform action, varied in effect according to the peculiar circumstances under which the secretory productions modify the nature of the developments.

This extension of the placentary sheath may be either complete as I have described it, or only partial: such a partial expansion is known to occur in *Turneraceæ*, and the circumstances under which it is there developed, offer still further confirmatory proofs of the placentary origin of the arilliform expansion in the manner above detailed. St. Hilaire in his 'Flora Bras. Merid.' pl. 120, figs. 4 and 5, exhibits the seed of *Turnera hermannioides*, where the raphe proceeds from the hilum, one-third way long its ventral face, like a cord: beyond this to the summit, and half way down the dorsal face, it spreads in the form of a broad fleshy plate or incomplete tunic. The same development is shown in plate 121, fig. 5, where, in the seed of *Turnera genistoides*, the raphe is seen to extend above half way from the hilum, as a cord, whence it expands as far as the summit, in the form of two broad auricular plates, nearly the length of the seed, one lobe being seen upon each of the lateral faces of the testa, forming, as in the preceding species, a partial fleshy envelope. Another instance of the enlargement of the placentary sheath occurs in *Asarum*, called by Gærtner an epiphysum†: Dr. Planchon also describes the seed of *Asarum Canadense*‡, as being greatly swollen upon its ventral face, along the line of the raphe, by a large glandular mass extending from the base to the apex, and filled with oily vesicles, as in the fleshy coating of *Magnolia*; this he denominates a strophiole, and

* Linn. Trans. xxi. tab. 26. figs. 22 & 31. † Gærtn. de Fruct. 48. tab. 14.

‡ Mémoire sur les développements des vrais et des faux arilles, p. 34. pl. 2. figs. 10 & 11.

Endlicher calls it a fleshy raphe, but this origin is evidently due to the same source as that of the outer tunic of *Magnolia*.

It is here necessary to point out the distinction between the different kinds of arilliform coatings of the seed. We have strong evidence to show that the scarlet covering in the *Clusieæ*, *Magnoliaceæ*, &c., is derived from a growth of the placentary sheath, which is a production of the funicular cord, whose origin is coæval with the anatropal inversion of the ovule: other cases however occur, where another still more exterior development is generated at a subsequent period: this is well known to proceed from the main placenta, or more often from the short funicular cord, which is the foot-stalk of the placentary sheath by which the ovule is attached, sometimes forming a thick cup as in the *Sapindaceæ*, &c., or at other times extending itself like a fleshy, coloured plane sheet completely enveloping the seed, as in the *Tovomiteæ*, or which form branching fleshy segments embracing the seed, as in *Myristica*, *Samydaceæ*, &c. These several varieties derive their origin from a growth of the placenta and are not developed from the original coats of the ovule; they are therefore arilliform in their nature, but as they are produced under different circumstances, I propose to confine the term aril (arillus) to the kinds of coating last described, always void of spiral vessels, and to denominate that sort found in the *Clusieæ*, *Magnoliaceæ*, &c., the arilline (arillinus), in which the vessels of the raphe are always imbedded. Both may and often do exist at the same time, in the same seed, or they may make their appearance independently of each other.

There is said to be still another kind of extraneous fleshy coating, produced over the testa in the manner first pointed out by St. Hilaire, to which he gave the name of false aril, and which was afterwards ably investigated by Dr. Planchon, who substituted for it the name of arillode*. This tunic is described as originating in the expansion or reversion (*dedoublement*) of the mouth of the exostome or foramen of the primine, which gradually extends itself over its whole surface, and forms an extraneous envelope around the testa. The formation of the arillode from such a source, rests upon the authority of Dr. Planchon, to which I attach its due weight; and although in support of his views, he described, with great minuteness†, the gradual formation of the arillode in *Euonymus latifolius*, it is certain that in drawing the conclusion that the arillode proceeds from the extension of the exostome, he expressed at the same time some misgiving on the subject‡. Examining therefore the details as there represented, and comparing these with my own observations on the seed of *Euonymus*, I think it may be inferred, with equal, if not with

* Mem. ante cit. p. 10. † Idem, p. 7.

‡ "En disant que ce dernier sac (le faux arille) procède uniquement de l'exostome, peut-être ai-je un peu sacrifié l'exactitude à la clarté. Comme l'ombilic, en effet, est très voisin du micropyle, l'expansion arilliforme partant des bords de ce dernier, devrait rencontrer dans le funicule un obstacle à son extension et offrir une solution de continuité. Mais c'est là au contraire *que l'expansion est la plus épaisse, et même elle adhère avec la base du raphe sur une partie de sa longueur de manière à ce qu'elle semble sur ce point naître de cette dernière partie.* Il faut donc nécessairement, pour expliquer une pareille disposition, admettre *une soudure congeniale entre l'expansion et le funicule.* Je crois devoir ajouter pour prévenir tous les doutes, que chez les *Euonymus, le micropyle est fort difficile à voir, lorsque l'ovule est déjà très développé, parceque le faux arille est plissé autour de son ouverture, et la cache complètement*: mais en détachant avec soin l'enveloppe accessoire, on peut facilement s'assurer qu'elle naît des bords de l'exostome." —*Loc. cit.* p. 9.

greater probability, that the extraneous coating is produced from the funicular cord, rather than from the foramen or micropyle of the primine, and in such case the arillode would not differ from the aril.

I have had no opportunity of examining the ovule during its growth, but have lately observed ripe and living seeds of *Euonymus Europæus*. Here the outer coating is entire fleshy and scarlet, with a smooth inner skin, and we find beneath it, another polished, thinner, though somewhat fleshy tunic, that closely adheres to the seed. If this tunic be removed carefully from the thin pergameneous testa, it will be found to consist of two delicate reticulated pellicles, having cellular and fleshy matter interposed between them, the raphe being completely immersed in its substance, in the form of a simple cord, which originating at the basal hilum, proceeds along its face to the apex, where it pierces the inner pellicle of this tunic, passes into a small opaque speck in the summit of the testa (the diapyle), and is lost in the chalaza of the inner integument which is adherent to the shell. Here we have demonstrative evidence of the nature of these several envelopes; the outer coat is manifestly a true and entire aril, for we cannot suppose it to be a development of the primine, that is to say, an extension of its exostome, as Dr. Planchon almost doubtfully concluded, because it is altogether free from, and exterior to a more internal tunic which encloses the raphe: it follows, therefore, as a necessary consequence, from the position of the nourishing vessels, that it must be a production emanating from the main placenta or a growth from the funicular support of the seed. The fleshy epidermoid tunic which encloses the raphe, and which immediately invests the pergameneous shell, appears to be an arilline, resulting from the growth of the placentary sheath: the thin pergameneous shell is, of course, the true testa, marked at its base by a small prominent nipple, close to the hilum, which is no doubt the thickened border of the true micropyle figured by Dr. Planchon, and from which he inferred that the growth of the aril had emanated: the apical speck through which the vessels of the raphe penetrate, is the diapyle: it is hardly necessary to add, that the radicle of the embryo, enclosed in albumen, points to the micropyle, while the extremities of the cotyledons are directed towards the diapyle. I do not find the aril pervious in the apex, as stated by Gærtner, and as figured by Dr. Planchon in another species, although this, no doubt, sometimes occurs; but in the instance above mentioned, the inner skin of the tunic, though slightly crumpled, is entire, while its outer pellicle is deeply plicated in flattened folds, so that the aril appears cleft into numerous fissures externally.

Among the many interesting facts detailed by Dr. Planchon in the work just quoted, we meet (*loc. cit.* p. 25) with an account of the circumstances under which the seeds of *Opuntia* become covered by two distinct extraneous envelopes, both exterior to the testa: the first is a somewhat thin, hard, coriaceous tunic, according to his observations; the second is a soft, mucilaginous, pulpy coat by which the former is encircled. The growth of the former was traced by Dr. Planchon from the period of the anatropal inversion of the ovule, which was carried to an extent of a complete gyration, so that the placentary sheath I have before described, appeared at first like an annular band around the periphery of the ovule; from this ring, on both sides, membranaceous expansions were seen gradually to extend themselves over the intervening spaces, until they met in the

centres, and thus formed one complete tunic, which finally assumed the solidity and texture of a crustaceous shell, which he called a "false testa": this again became enveloped by a second placentary extension, in the form of a transparent soft pulp. These facts had been previously authenticated by the careful observations of Gasparini*, who describes, with great apparent accuracy, the curious phænomena attendant on the growth of the ovule of *Opuntia*, from its earliest development to the state of its ripe seed. After its anatropal inversion, the ovule is seen suspended by its short funicular cord (podosperm) from the hilum, which cord, in form of a placentary sheath, or thick cylindrical filament, is seen to extend itself round it, until it encircles the ovule like an annular ring: from this ring, on each side, a distinct membrane, at first very thin, expands itself by slow degrees, until at length, on both sides, it becomes extended in a complete tunic, over the entire surface of the ovary. After the period of fecundation, he farther observes, if we watch every now and then the growth of the ovary, during its transformation to the state of seed, we see the tunic just mentioned, as well as its very short podosperm, become covered, little by little, with a pulp. In proof of the fact that the production of this more external tunic originates in the extension of the podosperm, he states that sometimes, in some ovules, from some unknown cause, the above-described annular prolongation of the placentary sheath is not formed, and in such case the seed is not covered with the usual pulpy envelope. Some explanation, however, is here requisite, which I am enabled to give from the examination of the large seed of a species of *Opuntia*, collected by me in Chili many years ago. This has convinced me of the correctness of the details given by Gasparini and Planchon, with this exception, that the thin pellicular membrane, which both actually witnessed in the act of its growth and extension over the primine, and which the latter imagined became converted into the thick osseous shell, is no other than the intermediate epidermoid tunic, which I found still covering the shell. We may feel assured that the deposition seen of osseous cells, to form the crustaceous shell, took place in the substance of the primine, and not in its arillinar covering, as Dr. Planchon inferred, for Gasparini makes no mention of such an occurrence. That such is the case, is manifest from the position of the raphe, and it is not less clear, from the phænomena observed, that the membrane, as they saw it in the progress of its growth, is a production of the placentary sheath, and is therefore of the nature of an arilline. So, in like manner, the pulpy envelope emanates from the placentary sheath or funicle; and that such is really its origin is proved by the curious fact related by Gasparini, that when, as it sometimes happens, the placentary sheath is unformed, no growth of pulpy matter takes place over the seed. From the circumstances above detailed, we may safely conclude that the hard crustaceous shell in the seed of *Opuntia* is its testa, that its annular ring is the raphe, and that the intermediate tunic coating the testa is an arilline; while the more exterior pulpy envelope, whether originating in the placentary sheath or the funicle, is still an aril, because it is void of spiral vessels.

Another striking confirmation of the fact of the gradual increment of the fleshy coating over the primine, is cited by Dr. Planchon, and is the more important, because it occurs in *Clusia*, and bears immediately on the question at issue. In the work before

* Osservazioni intorno alla struttura dell' arillo. Rendiconto dell' Accad. delle Scienze di Napoli, an. 1843, p. 260.

quoted (p. 31), as an instance of the progressive formation of the false aril, he describes and figures (in plate 2. figs. 7 & 8) the ovule of *Clusia flava*, which he examined after the fall of the corolla, at which period he observed that the primine adjoining the funicle became enveloped for a quarter of its length by a cup-shaped arilliform process, and there can be little doubt that this expands into the entire fleshy coating, which at a later period we know envelopes the testa in the manner I have described in the *Clusieæ*.

M. Dutrochet, a very able physiological botanist, in discussing the nature of the aril, denies that its growth proceeds immediately from the placenta, and declares his conviction, formed after many years of patient investigation of the subject, in the following words:—"L'opinion qui me paraît aujourd'hui la plus conforme à l'observation, est que l'arille est une extension de la partie inférieure ou de l'enveloppe corticale du funicule*."

Mirbel has furnished us with evidence of great importance in the solution of this inquiry: he minutely describes the growth and development of the ovule of *Cucumis Anguria*, in which he observed, after the period of its fertilization, the production of two distinct layers of cellular tissue over the primine, originating, no doubt, from an emanation and extension of the placentary funicle. His words are, "deux couches de tissu cellulaire, qui n'appartient pas primitivement à l'ovule, mais qui s'applique à sa surface et finit par lui servir d'enveloppe comme ses téguments propres†," thus affording unquestionable evidence of the extraneous growth of the arilline, evidence since confirmed by the observations of Gasparini and Planchon. I shall be able to show that the crustaceous tunic of the seeds of the *Cucurbitaceæ*, hitherto held to be the testa, as well as its immediate soft envelope, are both of arilliform origin, and that the true integuments resulting from the primine and secundine of the ovule are to be found in the membrane that immediately invests the embryo, and which has always been considered the tegmen: this fact is attended by some curious phænomena which will be detailed in another place, where I will adduce many instances of the anomalous development of the raphe. I will, however, here allude to the peculiar structure of the outer tunics in many of the *Cucurbitaceæ*: if the seeds of *Citrullus*, for example, be macerated in water, the outer shell will be found to consist of three distinct parts, which may be termed the epiderm, the mesoderm, and the endoderm. The epiderm is pellicular, transparent, and under the lens is seen marked by large areolar reticulations; the mesoderm is always fleshy, and composed of parenchymatous, frequently mixed with pleurenchymatous deposits; the endoderm, hitherto considered as the testa, is crustaceous, and consists of transverse hollow cylinders closely compacted and agglutinated together. The epiderm is a continuation, and a dilated termination of the external sheath of the umbilical cord; the mesoderm is also a continuation of the pleurenchymatous fibres of the funicle, where they serve to protect the more delicate spiral vessels of the raphe; but the crustaceous endoderm is a distinct deposit within the vesicle of the epiderm, forming a compressed and indurated sac, enclosing the seed, and always open at its mouth (the hilum), within which is a space filled with loose cellular tissue, which is also generally extended over the internal surface of the endoderm. These three deposits must be formed at a period subsequent to the fertilization of the ovule, as will be evident from the copious details, illustrated by

* Mém. Mus. viii. 273.

† Mém. Acad. Paris, ix. 622. tab. 1. fig. 10 *e*; fig. 11 *h*.

admirable figures, of the growth of the ovule recorded in the valuable Memoirs of Brongniart and Mirbel, and, as will be seen, proved by the observations of the latter, cited in the foregoing page. It is not more unreasonable to conceive that the osseous deposit, forming the crustaceous covering, may in some cases be secreted in the arilliform coating, as well as in the primine of the ovule; in both instances, the secreted matters must pass through the same channel, and be supplied by the same vessels of the funicle, and such depositions at one point, instead of another, are probably regulated by the nature of the pre-existing tissues. In *Zanonia* and *Feuillæa*, the arilliform nature of the outer coating is better shown by the membranaceous state of the tunic, which is extended like a winged covering over the seed.

From these circumstances we may infer, that the arilline need not necessarily be always fleshy in its nature, as in *Magnolia*; but that it may be either membranaceous, gelatinous, coriaceous, or even osseous in its structure. Thus I have found from the position of the raphe, that the hard highly-polished tunic of the seeds of *Drimys* and *Illicium*, usually regarded as testa, should be held to be a true aril: thus also the coriaceous coatings of many seeds will in like manner be found to be arilliform in their origin. Of that kind of seminal coating where the arilline is intimately combined with the testa, and where the raphe, greatly branched, lies imbedded between them, forming a compound tunic analogous to the structure already described in the *Tovomiteæ*, a very remarkable instance occurs in the *Oleaceæ*, where the raphe, instead of being spread into numerous branching nervures, exhibits itself by infinitely minute ramifications, as a dense network of most delicate spiral vessels, crowded together into a cottony web, like that of a spider's cocoon, and fills up the entire space between the testa and arilline; these tunics, aided by this interposition, are closely agglutinated into an apparently simple coating, but by maceration they may be separated from each other, and the interposed network may be drawn out into innumerable elegant spiral threads. This structure I have found in *Tessarandra* and *Olea*, and it probably exists in other genera of the family. Nearly the same development occurs in *Casuarina*, where a thick web of spiral fibres is found interposed between the crustaceous testa and the outer membrane, which is extended over it in the form of a wing. This structure, noticed many years ago by Mr. Brown, and at that period described as a singular occurrence (Gen. Rem. p. 40), has since been confirmed by Schleiden, and figured in Schnitzlein's 'Iconographia' (Gen. 86). The pellicular coating of the seed, here extended in the form of a wing, which covers the excessive development of the raphe, will probably be found to be an arilline.

We have a good illustration of the arilliform nature of the external coating of the seed, under somewhat variable forms, in the *Passifloraceæ*. In *Tacsonia pinnatistipula* I found the seed invested by a mucilaginous pulpy envelope, which dries into a loose pellicular vesicle, quite detached, leaving a considerable vacant space between it and the osseous testa, in every part save at a small point at the base, and at another in the apex: this pellicle shows no vessels of any kind, except in its longitudinal raphe, which is imbedded in its substance, appearing as a prominent white nerve, running from the basal hilum to the summit, where it finds a passage through a caruncular spot (the diapyle) in the apex of the testa, beneath which it becomes lost in the chalaza of the inner integument. In

Ryania (*Patrisia*), as shown in Delessert's 'Icones,' iii. tab. 14, the seed is covered by a similar arilline, and along the whole length of a similar longitudinal raphe, a lateral cupular fleshy expansion is developed, manifesting the coexistence of aril and arilline, emanating from the same origin. Both these developments also occur in *Paropsia*, where the seeds are suspended by a long funicle, which, at the hilum, is expanded into a fleshy cup, that envelopes the lower half of the seed. In *Acharia* the longitudinal raphe becomes distended on each side, forming a lateral gibbous process (Ann. Nat. Hist. iii. pl. 9. fig. 15) analogous to that before referred to in *Asarum*. In *Modecca palmata* an entire and very thick fleshy tunic invests the osseous testa, marked by a prominent longitudinal keel, enclosing the raphe (Wight, 'Icon.' tab. 201. fig. 12, 13, 14, &c.), and in *Modecca Wightiana* (id. tab. 179. fig. 3) we see precisely the same development, with the addition of another crenated hemispherical fleshy cup, covering the base of the seed. This is also seen in *Modecca australis* (Endl. 'Icon.' tab. 115). In all these cases, the raphe is perfectly free from the testa, and always forms part of a more external tunic more or less adherent to it, the arilliform nature of which has never been doubted; the structure is quite analogous to that found in *Magnolia*, &c., and distinct from the still more external development, the true aril.

The mass of evidence here adduced, strengthened by the observations of botanists of high repute, showing the nature of the several metamorphoses which accompany the production of the raphe under its different forms, indicate the real placentary origin, whether mediate or immediate, and therefore the arilliform character of the several extraneous tunics, which assume such various textures and conditions around the testa,—restricting this latter term within the limit usually assigned to it—a simple development and growth of the primine of the ovule. The question appears to me so simple and manifest, that I should have considered it unnecessary to enter into such full details in its support, if this point of structure had not been so positively denied by the high authorities to which I have referred: a desire for the solution of the truth has alone induced me to extend these observations to a greater length than otherwise would have been requisite. Many other interesting topics of physiological inquiry are connected with the farther consideration of this subject, and I have prepared another paper, in which are discussed many of the phænomena attendant on the peculiar direction of the raphe, especially in reference to the anomalies before alluded to, in *Stemonurus*, *Anona*, the *Cucurbitaceæ*, and other instances, with a view of tracing the causes of such unusual deviations from the ordinary course of structure.

EXPLANATION OF THE FIGURES.

Tab. XIX.

Fig. 56. Represents an anatropal ovule of *Magnolia*, after Dr. Asa Gray, seen on its ventral face.

Fig. 57. The same viewed sideways.

Fig. 58. A vertical section of the same. In all these the letter *a* shows the placentary sheath, enclosing *b*. the spiral vessels of the raphe; *c*. is the primine; *d*. the secundine; *e*. the tercine or nucleus; *f*. the gangylode; *g*. the hilum.

Fig. 59. Is a longitudinal section of the ripe seed of *Magnolia*.

Fig. 60. Is the crustaceous testa, cleared of its fleshy covering, viewed sideways.

Fig. 61. The same seen on its ventral face, showing the groove formed by the pressure of the raphe.

Fig. 62. The inner integument, covering the albumen. In all, the same letters refer to *a*. the scarlet arilliform outer coating, being an expansion of the placentary sheath seen in figs. 56, 57 & 58, which has grown over and covered the primine, and now completely envelopes the testa; *b*. the raphe; *c*. the testa or development of the primine; *d*. the tegmen, or inner integument, resulting from the secundine; *e*. the albumen; *f*. the diapyle or scar of the gangylode, through which the raphe passes to reach the chalaza; *g*. the hilum; *h*. the funicular cord; *i*. the chalaza upon the extremity of the inner integument, where the raphe is lost; *k*. the embryo imbedded in albumen:—*all much magnified.*

Fig. 63. Is a seed of *Licania* removed from its pericarpial covering:—*nat. size.* *a*. the tunic formed of three adherent membranes: the outermost is the arilline, the intermediate one is the testa, the innermost is the tegmen; *b*. is the hilum; *c*. the vessels of the raphe, interposed between the arilline and testa, and dividing into continual ramifications, which spread over the whole area of the seed: they all branch from the hilum, which is situated at the extremity contrary to that of the chalaza, or point corresponding to the original base of the ovule, showing that these vessels must be exterior to the real testa, and enclosed within another distinct integument; for if they were included within the substance of the testa, they would branch from the contrary extremity at the point corresponding with the original base of the ovule, the only point in which these vessels could have penetrated the primine, and therefore the testa.

Fig. 64. Is the exalbuminous embryo, also *nat. size*; *d*. the cotyledons; *e*. the radicle, placed near the hilum.